CHAPTER 9

Interactions Between Tillage and Earthworms in Agroecosystems

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CONTENTS

9.1 INTRODUCTION

For organisms that utilize the soil as habitat, a change in agricultural land use affects nearly every component of the soil ecosystem. Changes in the abiotic and biotic features of the soil ecosystem influence not only the numbers but also the types of organisms in the soil. The structural and functional aspects of agricultural systems are addressed in the wider view of ecology, in particular agroecosystems that are managed ecosystems, with abiotic and biotic features manipulated to promote maximal primary crop production. To achieve high levels of plant production, various inputs to the agroecosystem are necessary. These can include soil management and fertility amendments and generally involve the manipulation of soil and crop residues through some form of tillage.

Compared to other soil macroinvertebrates, the role of earthworms in the regulation of ecosystem processes is well recognized in the literature.[45,50,51,97] A renewed interest in the interactions of these animals with both the biotic and abiotic components of agricultural ecosystems has gained momentum in the last 20 years. Earthworms may regulate, mediate, or facilitate basic processes in soil ecosystems, so soil interactions are included in the sphere of the earthworm's influence (Logsdon and Linden, 1992). In support of this growing body of research, it has been suggested[30,112] that earthworms can play a role as indicators of agricultural sustainability and soil quality and as bioindicators in ecosystem-level studies of pollution fate and transport and functional relationships. Fragoso et al.[58] asserted that earthworms play an important role in the enhancement of agroecosystem productivity. However, this may be only to the extent that the activity of a particular species is both associated and synchronized with critical periods of root elongation, crop growth, and nutrient demand. Earthworms have been linked to improvements in crop production in both temperate[50,144] and tropical agroecosystems.[66,93] Certain species of earthworms are also associated with promoting improved availability of micronutrients. Not surprisingly, since the goal of any production agroecosystem is to provide optimal conditions for plant growth and biomass production, these same conditions simultaneously tend to improve conditions for the retention and dispersal of earthworm populations.

Edwards and Bohlen[50] listed the four main inputs into any agricultural management system as tillage, crop selection and sequence (i.e., rotations), fertility, and pest management. These inputs can change both the range of habitat type and the extent of resource distributions, thereby regulating the structure of earthworm communities. Crops provide different types of soil cover, extensive or consolidated root systems, and different needs for nutrient requirements and biomass production, which affect soil conditions and the amounts of organic matter returned to the soil. Tillage alters the physical, chemical, and biological aspects of soil ecosystems. By the same token, periodic tillage can change environmental conditions and thereby influence the period or pattern in which earthworm populations may develop. Disturbances due to tillage can alter the relative proportions of different earthworm species and change population sizes due to a decrease in the availability of food resources, increased intra- and interspecific competition, and mortality from either the direct effects of tillage or indirect effects that include predation,

desiccation, or exposure to agricultural chemicals. However, Hulugalle et al.[76] considered that the size and structure of soil invertebrate communities, including those of earthworms, are more a function of soil microclimate and the type and extent of pesticide applications rather than the type of tillage or cropping system. However, Tarrant et al. (1997)[149] observed no differences in earthworm responses to either full recommended or 50% insecticide application regimes. Overall, pesticide regimes can be important, and this bears consideration in the management of any agroecosystem.[50]

Through their activities in burrowing, foraging, and casting, earthworms are a unique group of soil-inhabiting organisms. Moreover, few other invertebrates have an ecological function that is matched so well with their size and other physical attributes,[2] which enables them to literally plow the soil, bury organic matter, and improve surface horizons through increased macroporosity, aeration, and infiltration, and by spreading microorganisms, organic matter, and nutrients throughout the soil. Since these activities occur within the soil system, there are many interactions between soil physical, chemical, and biological factors, and earthworms are considered to be key organisms in the integration of these factors.[82]

Earthworms have been shown to influence the overlapping chemical, physical, and biological components of soil ecosystems, through their interactions with soil structure,[56,73,79,85] water balance,[157] microbial activity,[19,23,126] organic matter cycling,[14] nutrient cycling,[77,115,145] and in the restoration of degraded ecosystems.[17,141,158,167] Due to the broad range of interactions that earthworms appear to have with the agricultural soil environment, much of the research related to earthworms has necessarily become interdisciplinary. The earthworm is a unique organism that focuses and integrates the disciplines of biologists, agronomists, and ecologists. However, relatively few investigators have addressed the interactive relationships among tillage, earthworms, and the overall agroecosystem.

9.2 EARTHWORM ECOLOGY

Due to the wide range of conditions and habitats available, agroecosystems always contain more than one earthworm species. By their common focus on production of annual crops and periodicity (or absence of) tillage, agroecosystems are, of necessity, locked into the equivalent of a perpetual early succession, which is punctuated by relatively frequent disturbances of the soil system. In spite of such periodic disturbances, which often reduce the total numbers of earthworms, most soils and cropping systems support some type of earthworm community. Certain species, particularly lumbricids, are better adapted or have habits more suited to the improvement of agroecosystems.[16,139] However, the frequency and extent to which a soil ecosystem is disturbed can have complex effects on earthworm populations. Disturbance of earthworm communities alters the patterns of growth, reproduction, and competitive relationships among earthworm species.[141] In many instances, a disturbance will alter the habitat such that it may become more appropriate for exotic species. These species are often generalists and may also possess adaptations to

agricultural manipulations, and they can therefore establish more easily under degraded soil conditions. There is some evidence that shifts in land use in various agricultural soils, and consequent change in soil properties, have led to the dominance of exotic species, particularly in the U.S., with a concomitant decline in populations of endemic species in these soils.[9,81] For instance, in a study of earthworm feeding ecology in a Kansas prairie,[78] noted that earthworms belonging to the family *Lumbricidae* tended to displace other earthworm species competitively and eventually come to dominate the earthworm community.

The interactions among different ecologically functional groups of earthworms can occur through traditional ecological interaction like competition for abiotic (e.g., space) and biotic (e.g., crop residues for food) resources. In general, these interactions can lead to uniquely structured earthworm communities and, through the domination of certain ecological groups, influence soil processes differentially and consequently affect the availability of resources in soil systems. Earthworms have been termed anecic, epigeic, and endogeic ecological species.[25,50,93] These ecological divisions are based mainly on their reproductive rates, food preferences and foraging habits, and other behavioral or morphological characteristics. Such general classifications are not universally accepted since some species may have attributes that are typical of several of these ecological groups. The activity and habits of a given species may tend to change with their habitat or growth stage, blurring the general distinctions ascribed to these ecological groups.

The anecic species are characterized by a larger relative size and a tendency to burrow vertically into the soil and consolidate and transport coarse organic matter resources from the surface into their burrows. A common example of an anecic species is *Lumbricus terrestris* L. Other earthworm species such as *Lumbricus rubellus* Hoff., which are defined as epigeic species, are smaller than anecic species and tend to be active at the soil surface, where they forage within the litter layer. In response to the rapidly changing conditions that frequently occur at the soil surface, epigeic species usually have faster reproductive rates and higher metabolic rates.[14] According to Perel and Neilson et al.,[110,116] the anecic and epigeic species are usually more similar to each other in their habits than to the endogeic species (Table 9.1). Both ecological groups are considered to be humus formers due to their reliance upon coarse or partially decomposed organic matter for food. Endogeic species are often referred to as geophages and tend to be humic feeders.[116] As their name implies, geophagous species such as *Octolasion tyrtaeum* (Savigny) and *Pontoscolex corethrurus* (Müller) consume large quantities of soil and particulate organic matter as they burrow horizontally through the mineral soil at depths down to 15 cm.

Earthworm feeding ecology is the basis of these traditional functional divisions, and this can generally be determined by an analysis of gut contents and diets and by feeding observation. Perel[116] suggested that a more flexible classification might be to divide earthworms functionally as humus formers and humus feeders. In support of this concept, Neilson[110] compared soil $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios produced by earthworms collected from deciduous and coniferous woodlands, pastures, and arable land and considered that the traditional functional classifications (i.e., anecic, epigeic, endogeic) were not isotopically distinct and at the species level were more a function of the specific habitat. The approach of Neilson[110] generalized earthworm

Table 9.1 Levels of Significance Show Correspondence and Differences among Habitat and Ecological Classifications

Site	Epigeic vs. Endogeic	Epigeic vs. Anecic	Endogeic vs. Anecic	Humic Former vs. Humic Feeder
		δ^{15}N (o/oo)		
Arable	0.02	NS	NS	0.02
Coniferous woodland	<0.001	0.01	<0.001	<0.001
Deciduous woodland	<0.001	NS	NS	0.01
Permanent pasture	NS[a]	NS	NS	0.03
		δ^{15}C (o/oo)		
Arable	0.001	NS	0.01	<0.001
Coniferous woodland	<0.001	NS	<0.001	<0.001
Deciduous woodland	<0.02	NS	NS	0.02
Permanent pasture	0.04	NS	0.001	<0.001

[a] NS = not significant at $p > 0.05$.

As per Bouché,[25] Perel,[116] for both δ^{15}N (o/oo) and δ^{15}C (o/oo) abundance.

Source: Adapted from Neilson et al., 2000.

functional group classifications on the basis of feeding ecology and showed that the traditional categories are more the consequence of the reactions of a particular earthworm species to a given habitat. Kobel-Lamparski and Lamparski[89] suggested that ecologic groupings may also change with age, so that some species, such as *Lumbricus badensis* (Mich.), can change from an epigeic to an anecic type of activity over the course of its development.

The habitats of anecic and epigeic earthworm species frequently overlap at the soil surface. Yet, due to their large size and other adaptations, anecic species tend to be more flexible in their ability to change and modify their habitat than epigeic species. However, the smaller size of epigeic species may be scaled better to extremely dynamic microhabitats. Among those species whose ecological niches overlap, these interactions can also lead to competition and displacement. There is some evidence that epigeic species, such as *L. rubellus*, may be displaced[145,157] in the presence of *L. terrestris*. Yet under similar experimental conditions, endogeic species such as *Octolasion tyrtaeum* (Savigny) appear to benefit from the presence of *L. terrestris*.[131] Edwards and Lofty[52] reported significant negative correlations between the abundance of *L. terrestris* and *Aporrectodea longa* (Ude). In another instance, *L. terrestris* in the presence of *Aporrectodea tuberculata* Eisen produced no observable interactions.[157] Earthworms are sensitive to environmental conditions in agroecosystems and in many cases modify their environment and engineer local resource distributions to optimize their habitat. The term *heterochresty* has been used to describe an organism's ability to both create and use heterogeneity in local resource distributions. The word is derived from the Greek, where *heteros* is means "different," and *chrestikos* means "knowing how to use"[26,28] thus, this term may be particularly apt when applied to some species such as the deep-burrowing *L. terrestris*. Heterochresty generally describes the ability of a species to take advantage of

heterogeneity in the environment and make more heterogeneous a previously homogeneous environment. Both situations reflect an earthworm's response to ambient environmental conditions by changing them to its advantage.

With a few notable exceptions,[11,21,99,145] the spatial and temporal aspects of earthworm community dynamics and their interactions with tilled agroecosystems has not been well characterized. Whereas Ligthart and Peek[99] observed the dispersal of several earthworm species in time in a reclaimed polder, both Subler et al.[145] and Bohlen et al.[21] used direct manipulations of earthworm populations in agroecosystems as experimental treatments, which were then used to study the interactive effects of earthworms with their agroecosystem habitat. The merit of these studies, however, was principally the accumulation of data on earthworm population dynamics in disturbed ecosystems, thereby laying a strong foundation for understanding the complexity of earthworm–agroecosystem interactions. Most of these studies were performed in temperate climates, pointing out the need for similar studies in tropical agroecosystems. One reason for the relative dearth of information on earthworm ecology is that studies of earthworm community dynamics are difficult to achieve. On the other hand, there is a large literature regarding soil processes involving just a few species of earthworms or earthworm communities. It is on the basis of such process-level studies that we will attempt to integrate and relate a sometimes divergent body of research, particularly in terms of the effects of tillage on earthworms.

9.3 INTERACTION OF EARTHWORMS WITH ABIOTIC COMPONENTS OF THE AGROECOSYSTEM

Much of agroecosystem management has been concerned with the manipulation of abiotic soil features. Specialized traction and tillage equipment currently provide a high degree of control over abiotic soil conditions. Nevertheless, modern approaches call for a consideration of the effects of agroecosystem management on the soil biota, such as earthworms. Many workers have commonly found that the size and composition of earthworm populations can be correlated significantly with changes in soil water content and temperature[9,33,43] demonstrated that an improved soil environment was the most important factor in the promotion of earthworm growth and increases in earthworm populations. The fundamental abiotic features of the soil that are most commonly managed include, but are not limited to, soil water balance and aeration, temperature, pH (i.e., soil reaction or soil acidity), and soil structural conditions in the uppermost soil horizons. These abiotic factors often dictate the types and extent of tillage inputs, the need for liming, cropping patterns and rotations, and organic-matter management. Each of these abiotic inputs has distinct impacts on earthworm populations.

9.3.1 Impacts of Soil Water Management

Soil water management has direct effects on the extent to which a soil can support earthworm activity, which is usually unrestricted in areas where the volumetric soil water content is in the range of 25 to 30%,[8,50,97] which corresponds to the soil water content at field capacity in typical agricultural soils. However, the ephemeral nature

of soil drainage and recharge often tends not to provide optimal conditions for earthworm activity. In the absence of soil water uptake by crops, Auerswald et al.[4] reported that geophagous earthworm population abundance, under 5 years of bare fallow, was controlled by water stress over and beyond any food stress.

Although seasonal flooding of soils can influence earthworm populations, they are usually resilient to temporary submergence, and most agroecosystems are designed to take advantage of natural drainage pathways. In the absence of natural drainage, which is often the case for heavy soils, tile drainage is commonly used to allow unimpeded field traffic in field operations and promote more favorable soil water conditions. Long-term saturated soil conditions can be detrimental to earthworms, particularly when partial pressures of carbon dioxide and oxygen reach critical levels. Nevertheless, a wet soil usually relaxes behavioral restrictions on earthworms foraging at the soil surface. Additionally, once out in the open, earthworms are susceptible to predation and desiccation.

Earthworms contain 75 to 90% water by weight and exist in a critical equilibrium with the soil water. As a result of this dependence on moist soil conditions, dry soils may be more problematic to the earthworm than saturated soils. Earthworm behavioral responses to dry soils can involve physical migration into deeper soil or estivation. Although most earthworm species exude mucous compounds to facilitate their burrowing and to survive moderately dry soil conditions, an extended period of low soil water content or high matric suction can induce a state of diapause (estivation); if this dry period is protracted, they may die. Alternatively, some degree of desiccation can increase the cold-hardiness of certain earthworm species. Mortality due to a hard frost can be forestalled or prevented by a decrease in earthworm tissue water content, a depression of tissue freezing points due to higher solute concentration in the nephritic fluid, or a combination of both mechanisms.

Although earthworms differ widely in their tolerance of and response to desiccation, some generalizations can be made on the basis of earthworm ecological groupings. Anecic species and some endogeic species[34] can escape the drier surface horizons by moving deeper into the soil profile, where an increased proximity to capillary water from shallow water tables may provide regions of suitable soil water content. Earthworms can move laterally and concentrate between crop rows, where soil water resources are not tapped so much by crop root mass as they are closer to the crop row. Arguably, epigeic species are least prepared to deal with dry soil conditions since their surface-dwelling habitat provides little protection from dynamic surface conditions such as drying. The top 5 cm of soil is the most changeable in terms of soil water content and will generally reflect ambient conditions. The presence of coarse organic matter resources for cover at the soil surface or particulate organic matter to increase the water-holding properties of the soil can help to mitigate adverse conditions in populations of epigeic species.

Soil water content varies across soils and is an important determinant of earthworm activity in field soils. Zaller and Arnone[165] manipulated the soil water content in field plots and reported that populations were not affected by an additional 28 cm year^{-1} rainfall over ambient levels. However, soil water content is perhaps not a universal, or even ultimately reliable, indicator of soil water status. This is especially true with regard to limits on those kinds of earthworm activity that are driven by

the soil water balance. The central issue is the extent to which soil water is available to the earthworm[37] rather than how much water there is in the soil. Differences in soil texture, and the corresponding degree to which soil water adheres to soil aggregates, is one reason why not all soil water is equally available to the earthworm. The energy required to extract water from the soil is known as the matric potential and may offer a more general measure to indicate which ranges of soil water or matric potentials required for earthworm activity. Soil water suctions from 0 to 1585 kPa have been reported as possible thresholds for earthworm activity.[48,91] In laboratory microcosms containing different soil types, Doube and Styan[48] showed that different earthworm species responded differently to changes in soil water content and soil matric potential. The unpigmented and strongly endogeic species *Aporrectodea rosea* (Savigny) tended to move towards wetter soil when it encountered a matric suction of 300 kPa, independent of soil type. However, for *A. trapezoides* (Dúges), which combines both epigeic and endogeic habits, the threshold soil matric potential was 15 kPa for a sandy loam soil, 25 kPa for a loam, and 300 kPa for a clay soil. Although no general matric potential threshold for earthworm activity has been determined, earthworms with more flexibility in their habitats or an increased sensitivity to moisture changes would be less sensitive to shifts in soil water status. With regards to managing, promoting, or monitoring earthworm activity, the suction-cup tensiometers that are typically used for timing irrigation can help to gauge when and where earthworm populations may be active.

The relationships of soil–water balance to earthworm activity in agroecosystems is complicated by management impacts, which can alter soil–water balance across seasonal time scales and at short spatial scales in row-crop agroecosystems. The amount of water stored in the soil is linked to crop type, crop growth phase, the degree to which water is removed over a season (i.e., evaporation and transpiration), and the replacement of soil water through the extent that precipitation infiltrates. However, most management techniques aim to promote retention of soil water. Minimum or conservation tillage can deemphasize the role of tillage in agricultural management. Reduction or elimination of tillage inputs decreases the amounts of soil water lost to evaporation and allows for the retention of some proportion of crop residues as surface cover. The maintenance of a plant canopy, surface cover, and higher levels of soil organic matter levels protects the soil in several ways. While the canopy intercepts and directs rainfall, surface cover mitigates against surface slaking and crust formation due to raindrops, which can in turn promote higher infiltration rates. Once water has infiltrated, a high soil organic-matter content can promote the retention and storage of water. The retention of plant residues on the soil surface, which is typical of no-till agroecosystems, can concomitantly decrease the amount of water that is lost due to evaporation and increase soil water content.[121]

The ways in which soil water is replenished are largely a function of the extent to which infiltration can occur. Tillage and pedogenic processes can fracture and separate otherwise massive structural units in a well-structured soil, leaving cracks and cleavage planes.[120] Clay et al.[36] pointed out that in ridge systems, the ridge can shed water into the furrow (i.e., interrow) region, increasing the soil water content of the furrow region.[6] However, concentrations of stemflow from crops (e.g., corn)

can direct water onto the ridge top, presenting more water to the more permeable ridge top, to replenish the in-row region. Crop canopies can also protect soils from direct impacts of raindrops, reducing soil crusting and enhancing infiltration properties. Although conservation tillage can decrease the amounts of nutrients or pesticides adsorbed[36] or lost by erosion or runoff, conservation tillage is usually associated with higher vertical infiltration rates. Infiltration in conservation-tillage systems can also operate through a wider range of overall larger pore sizes, leading to increased leachate volumes, which has implications for wider-ranging impacts on water quality.[10,35,55,134,157] Yet it is under no-till or conservation-till conditions that earthworm populations are most likely to flourish.

Infiltration of water into the soil in agroecosystems is affected considerably by interactions between earthworms and tillage. Biopores left by deep-burrowing earthworms form temporary or semipermanent zones of preferential flow. The continuous burrows formed by anecic species can significantly increase infiltration rates, the proportion of bypass flow,[135] and saturated hydraulic conductivity.[84] The contribution of macropore flow to overall leachate production and quality is an important factor in the production of leachates.[55,65,106] Leaching is a significant pathway for losses of soil water and dissolved nutrients from agroecosystems. Additionally, the fate of leachates is often to move to surface waters, where they may be considered pollutants. In particular, the activities of deep-burrowing earthworms have been linked to macropore networks in many soils[56,98,157,164] and under different types of agricultural management.[55,164] More recent work has established the important role of *L. terrestris* burrows in solute transport.[92,98,134,145] Although some types of burrows may be continuous, not all are connected to the surface, thereby altering the flow characteristics and composition of macropore water. Yet through true bypass flow, earthworm burrows can reduce surface runoff by providing preferential pathways for flow. Earthworm macropores have diameters in the range of 0.1 to 1 cm and can pass large amounts of water unimpeded via a mechanism typically known as preferential flow.

Bouché and Al-Addan[25] showed that earthworm inoculations into soils increased infiltration rates; soils with anecic species added exceeded those with all other species in their effects on infiltration. In a soil pot study, the addition of a mixture of epigeic and endogeic species resulted in a relatively uniform burrow network that extended throughout the soil to a depth of 21 cm.[59] The addition of anecic species to both chisel-plowed and no-till field plots led to a 4- to 12-fold increase in leachates as measured with zero-tension lysimeters.[145] In an agroecosystem that can support large numbers of deep-burrowing earthworms, the loss of soil water may itself be a source of stress on crops. Earthworm macropores are often a major pathway for nutrient losses from an agroecosystem.[98,134] The activities of deep-burrowing earthworms not only create preferential pathways for water and solutes but also play a major role in nitrogen cycling in agroecosystems.[14,145] Lachnicht et al.[92] showed that the addition of deep-burrowing earthworm species to a tilled silt loam led to the formation of macroporous channels, which conducted a latex solution to deeper regions of the soil, that preferentially compared with its movements in other earthworm population-reduction or control treatments. Additionally, Li and Ghodrati[98] showed that burrows of *L. terrestris* created continuous flow paths in laboratory columns, which conducted a nitrate solution, preferentially at low solute fluxes.

However, the role of surface connectivity may be an important factor in losses of nutrients and water from the soil surface. By blowing colored smoke through capped tile drains Shipitalo and Gibbs[137] identified surface-connected *L. terrestris* burrows, which were subsequently found to be a direct conduit for solutions of injected animal wastes into the tile drainage system, contributing to pollution of drainage and surface waters. Yet Stehouwer et al.[143] showed that the earthworm burrows were lined typically with organic matter and compounds that could adsorb compounds that might be otherwise lost through preferential-flow pathways. Farenhorst et al.[57] showed that earthworms foraging on residues contaminated with radiolabeled atrazine decreased the amounts of atrazine available for leaching and decreased the overall leaching of atrazine.

Although Shipitalo et al.[136] concluded that tillage had little effect on the loss or retention of nonadsorbed solutes such as nitrates, earthworm burrows that were not disturbed by tillage remained potential sinks for water, nutrients, and dissolved agrochemicals. The presence or relative abundance of earthworms with different burrowing habits can influence the creation or destruction of burrow networks[38,99] at different depths in the soil. However, the life spans of earthworms and their associated macroporous burrow networks are controlled largely by management issues such as tillage type and frequency.[83] Willoughby et al.[161] found that infiltration rates increased in no-till soils over those with conventional disk tillage, apparently in response to the presence of deep-burrowing *L. terrestris*. However, any contribution towards improved infiltration through the burrows created by *L. terrestris* was attenuated by periodic tillage. A lack of continuous macropores in the soil of chisel-tilled plots impeded infiltration at a depth of between 5 and 19 cm, which is a depth interval commonly tapped by crop roots for water.[164] Trojan and Linden[157] showed that tillage alone neither affected nor accounted for all of the movement of a dye that was allowed to infiltrate into rotary-tilled and no-till field plots inoculated with earthworms. Surface-connected burrows left by earthworm activity caused transport to and storage of water at greater depths. Partially incorporated crop residues also conducted water along edges, accounting for additional amounts of dye that infiltrated. Zachmann et al.[164] concluded that a greater degree of pore continuity and earthworm survivability in no-till soils combined to increase the abundance of surface- and subsurface-dwelling earthworms, which led to higher infiltration rates through a greater proportion of the soil profile.

9.3.1.1 Effects of Soil Temperature on Earthworm Populations

Fluctuations in soil temperatures can affect earthworm activity and abundance. Earthworms in temperate agroecosystems tend to favor habitats with a temperature range of 10 to 20ºC, with a temperature of 20ºC for optimal growth. Soil temperatures of 30ºC killed *L. terrrestris* after 14 d.[8,44] *Lumbricus terrestris* L. maintained in laboratory microcosms could tolerate short periods of temperature-induced stress, which influenced their growth positively.[125] Daniel et al.[44] reiterated that brief respites from periods of temperature stress may be sufficient to permit maintenance and survival of *L. terrestris* under compromised thermal conditions. Earthworm species

that are common in tropical agroecosystems have different adaptations and responses to heat stress. In a long-term field experiment, Reddy[123] demonstrated that extremes in soil temperature of vertisols and alfisols underlying a tropical savanna could explain a large proportion of the variance in numbers of the species *Barogaster annandalei* (Stephenson) and *Octochaetona phillotti* (Michaelson). These species were driven to soil depths of down to 45 cm by extremes in cold or heat. These extremes in soil temperatures tended to induce diapause, which was indicated as an important factor in the survival of these earthworm species.

However, soil temperatures in temperate ecosystems do not usually remain at extremes for long periods of time. Soil temperature usually follows periodic diurnal cycles, and the periodicity of these thermal cycles is increasingly damped by soil depth. The maximum temperature of the surface soil is also very dependent on soil texture, coloration, the extent and type of surface residue cover, soil water and gas balance, and soil structure. This indicates that, as with soil water relationships, earthworms able to live in a more flexible habitat are better equipped to change their positions in the soil profile so as to moderate and survive unfavorable temperatures. This may be an important feature of those earthworm species that are either pioneering colonization of agroecosystems or are able to recover from effects of tillage. Soil temperatures can be manipulated directly through tillage and the management of surface litter cover, lowering soil temperature.[121] Soil that is mounded or ridged exposes a greater part of the soil surface area to aboveground environmental conditions. The ridged soil tends to follow changes in air temperature more closely than plowed soils at the same soil depth. Regular ridging or bedding of the soil can raise soil temperatures in the early part of the growing season and thereby stimulate earthworm activity following an overwintering period spent mostly in estivation.

9.3.1.2 Effects of Soil Acidity on Earthworm Activity

Earthworm species differ widely in their ability to tolerate soil acidity (i.e., pH < 7); most arable soils are kept nearly neutral so as to promote the availability of nutrients. In intensive agricultural production practices, the use of acid-producing fertilizers such as ammonium sulfate, urea, or ammonium nitrate can influence earthworm activity by depressing localized pH levels in the plow zone. In Australian potato agroecosystems, which are intensive cropping systems involving large amounts of chemical inputs and heavy tillage, the recovery of earthworm populations was associated with an adjustment of soil pH by liming.[30] Any type of tillage that inverts the soil will bring deeper soils that are rich in leached cations closer to the surface, thereby regulating soil acidity. Some earthworm species have been shown to be well adapted to acidic soil conditions or otherwise equipped to modify their immediate environment to produce more favorable conditions. Henrot and Brussaard[69] reported that *Pontoscolex corethrus* and smaller eudrilid earthworms could persist in an acid ultisol under alley-cropped maize and cassava crops.[50,69] These species have shown some ability to moderate microsite soil pH through exudates from their calciferous glands,[50] production of mucilage, and the egestion of casts that can be more

neutral in pH than the surrounding soil.[166] In a laboratory microcosm, Mariño et al.[105] took *Lumbricus rubellus* (Hoff.) individuals from calcareous and acidic soils and transferred them to other soils to determine if individuals could adapt to nonnative soil acidity levels. The earthworms established successfully in them and demonstrated evidence of tissue calcium regulation in response to the different levels of soil acidity that they encountered. With some notable exceptions, earthworm intolerance to acidic soils is most pronounced at pH 5.[50] However, Mele and Carter[108] showed that a minor downward pH adjustment from a near-neutral soil pH had the effect of decreasing earthworm abundance by about 60% in a community composed of species from the families *Lumbricidae*, *Acanthodrilidae*, and *Megascolecidae*, in a xeralfic Alfisol. The dryland environment may have combined stresses due to soil acidity with water stresses. Although reclaimed mine spoil is not typically used for cropping, the popular use of earthworms in restoration may provide data on how earthworms react to acidic habitats. Scullion and Mallik[129] indicated that earthworms that were introduced to restored opencast mine spoils became established rapidly and were still present 9 years later. Vimmerstedt and Finney[158] showed that populations of *L. terrestris* added to a highly acidic (pH ~ 3.5) persisted for 5 years in a reclaimed shale mine spoil and for 10 years in a calcareous strip-mine soil. The introduced earthworms triggered a redistribution of organic matter into the soil and increased exchangeable basic cations by 50%, demonstrating that the earthworm played a significant role in moderating the acidity of its habitat.

9.3.1.3 Effects of Soil Texture, Type, and Depth on Earthworm Activity

Soils form the habitat of earthworm populations and can therefore exert a major influence on whether or not earthworms can naturally populate or adapt to them. Earthworm activity has been attributed to the development of horizons in no-till pedons[133] and a reclaimed peat soil.[27] Earthworm species can redistribute organic matter differentially into the soil matrix and profile[146] and bring soil to the surface in the form of casts,[7] resulting in a mixed humus profile. Although the depth of the uppermost mineral soil horizons does not limit the overall potential of agroecosystems, a shallow soil can affect the activity of some earthworm populations. Although Rossi et al.[124] did not observe any significant relationships between the abundance of the endogeic species *Polypheretima elongata* and the heterogeneity of soil, other workers have concluded otherwise. Hendrix et al.[68] reported that higher concentrations of silt-sized particles in soils had significant effects on earthworm activity. Nuutinen et al.[111] related soil textural properties that they measured on a grid to corresponding earthworm populations and reported that *L. terrestris* was usually associated with silty soils, whereas *Dendrodrilus rubidus* occurred most commonly where clay content was lowest. Silt particles tend to be incorporated into aggregates, increasing the variability of the pore size distribution with a corresponding increase in capillary pore water capacity, which is appropriate for sustained earthworm activity.

Depth of soil is an important factor in earthworm habitats. The impact of continuous tillage on different New Zealand soils was studied by Yeates et al.,[163] who

found that earthworm populations were at a minimum, and predatory nematode populations at a maximum, in both floodplain and common inceptisols, which are typically shallow soils with poorly defined horizonation. Nevertheless, earthworm populations were greatest under cultivations in both a Mollisol and an ochric Inceptisol, where soil properties were more favorable for earthworm populations and populations of predaceous nematodes were minimal. Accordingly, shallow soils are unlikely to provide the best habitat for some species of earthworms. Shuster (unpublished data) observed declines in manipulated *L. terrestris* populations in chisel-tilled agroecosystems underlain by shallow, floodplain soils (fluventic Hapludalf) in southern Ohio, USA. Relatively large numbers of *L. terrestris* were added twice a year to both chisel-till and a no-till ridged agroecosystems. It was clear from biannual population assessments that in the soil, regular additions were required to maintain populations of these anecic species. In the year after the earthworm additions were discontinued, very few surface middens were observed. The chisel-till cultivation offered fewer resources at the surface to earthworms, and the shallow water table saturated the soil profile with a greater frequency, leaving the *L. terrestris* without safe havens usually achieved through burrowing deeper, and instead were forced to weather the elements and respond to some degree of competition from other earthworm species at the surface. In contrast to chisel-till plowing, ridge tillage provided more resources (from an expanded rotation and reduced tillage) and a surface topography that apparently increased the amount and quality of the habitat for *L. terrestris*.

9.3.1.4 Effects of Earthworms on Soil Structure and Aggregation

Earthworm activity is often credited with altering the soil conditions for crop growth.[47,100] Earthworms have been observed to increase the number and water stability of macroaggregates, improve infiltration,[7,17,73,85,101] enhance macroporosity and infiltration,[133,147,157] and increase resistance to crust formation.[87] Historically, the presence of earthworms has been associated with improvements in, rather than degradation of, soil structure and its ability to support favorable cropping conditions. In particular, epigeic and anecic earthworm species have been shown to affect soil structure by foraging,[130,131] burrowing,[118] and casting.[132] Earthworms are active in processing raw organic residues into carbonaceous binding compounds,[154] which promote the formation of water-stable macroaggregates.[85,103] The working of the soil by surface-active earthworm species leaves casts that are intermixed in the soil, with little formation of burrows, and a cumulative increase in soil surface roughness. The increased variation in surface conditions mitigates against the formation of soil crusts.[87] However, Shuster et al.[138] showed that crop residue cover can be an important factor in maintaining surface soil conditions, particularly when surface-dwelling earthworm species are displaced by anecic species.

Earthworms create burrows by alternately exerting reciprocal radial and axially-directed forces. The resulting peristaltic motion drives the earthworm though the soil matrix; some species also literally "eat" their way through soil. Hirth et al.[71] reported that nearly 68 and 88% of burrows of *Aporrectodea caliginosa* and *A. rosea* (Savigny), respectively, were filled with casts. Keudal and Schrader[86] investigated

the differential pressures exerted by species from different earthworm ecological groups. It was determined that radial pressure was overall more important than axial pressure; the endogeic species showed the highest levels, with pressure in the range of 59 to 195 kPa, followed by the anecic (72 to 93 kPa) and epigeic (39 to 63 kPa) species. Earthworms alter soil structure through the formation of burrows, which also provide microsites that provide space and thereby facilitate root penetration.[51–54] Springett and Gray[142] presented evidence that the order in which the soil was colonized by either roots or earthworms changed with the distribution of earthworm burrows and the tendency for plant roots to elongate along earthworm burrow passages.

However, observations regarding the interactions between earthworms and any consequent facilitation of root elongation differ considerably. Sveistrup et al.[148] found that root penetration below the plow layer was almost entirely due to deep-burrowing *Aporrectodea longa* (Ude), *A. caliginosa* (Savigny), and *L. terrestris*. A study by Edwards and Lofty[53] reported improvements in root mass in direct-drilled barley stands after additions of *A. longa* and *L. terrestris* species. Pitkanen and Nuutinen[118] determined that in an unplowed field, the proportions of burrows intercepted by plant roots were 60 and 18% for the 15- and 80-cm depths, respectively. However, in a separate experiment, Hirth et al.[71] reported that ryegrass roots exhibited no preferential penetration into randomly placed artificial subsoil burrows filled with earthworm casts, instead elongating horizontally upon meeting the more impermeable subsoil layer. Overall, these experiments used undisturbed soil systems to test for effects of earthworms on macroporosity, which is used as a generalized term to cover burrow extent and abundance. Although increases in macroporosity resulting from tillage may be ephemeral, it is clear that earthworms play a major role in the porosity of the soil matrix between tillage events.

Due to its close relationship to total porosity, bulk density is an agroecosystem-level index of root elongation and the flow of air and solutes through the soil. Earthworms can decrease the bulk density of compacted soils through burrowing, mixing, and processing soil and organic matter and leaving casts that may be of lower bulk density than the surrounding soil.[84] However, highly compacted soils can, in some situations, restrict earthworm access to the surface.[12,84,167] In some tropical agroecosystems, the types of species can impact soil bulk densities. Populations of *Hyperiodrilus africanus* and *Eudrilus eugeniae* aided in the restoration of a degraded Oxic Paleustalf by decreasing bulk density.[151] However, Alegre et al.[1] considered the species *Pontoscolex corethrus* to be a “compacting species” as it increased bulk density in a typic Paleudult. The mechanism of such increases in bulk density was attributed to excessive activity of the endogeic species *Pontoscolex corethrus* in consuming small aggregates and casting larger, more compact aggregates. In a study similar to that of Alegre et al.,[1] Blanchart et al.[18] found that soil structure of a natural savanna was maintained through the activity of both *Millsonia anomala*, which formed macroaggregates > 0.5 cm, and smaller filiform eudrilid species, which egested aggregates sized 0.05 to 0.5 cm. Yet the removal of either species degraded the effects of the earthworms on soil structure significantly. In a soil pot experiment, Derouard et al.[47] reported that *Millsonia anomala* activity led to increased compaction and decreased infiltration, whereas *Chuniodrilus zielae* and

Hyperiodrilus africanus had opposite effects, while *C. zielae* and *M. anomala* had an intermediate effect on soil compaction. The lack of tillage disturbance in savanna and pot experiments may have allowed the species or communities with the most influence on soil structure to supply a full-range of stable aggregates. Nevertheless, the presence or absence of certain earthworm species has been demonstrated to impact soil structure strongly in untilled, tilled, and natural ecosystems.

9.3.1.5 Effects of Earthworm Inoculation into No-Till Soils on Root Growth and Yield of Cereals

Field experiments that artificially manipulated populations of earthworms in no-till soils demonstrated that earthworms could have significant effects upon the growth of cereal roots.[53] The major mechanism for these effects was the production of burrows lined with cast materials through which roots grew. In these experiments, typical field populations of deep-burrowing or shallow-working earthworms were inoculated into small plots that had been sterilized with dichloropropane-dichloropropene (D.D.®) on a site that had been cropped with cereals under no-till for six successive previous years. Inoculation with deep-burrowing species (*Lumbricus terrestris* and *Allobophora longa*) significantly increased barley plant populations (Figure 9.1, Table 9.2); the weight, height, and amount of cereal foliage; and the weight of roots, particularly in the upper 4 cm of the soil profile (Figure 9.2, Table 9.3). It seems likely that the lining of the earthworm burrow with casts rich in available nutrients may have contributed to this response. Most of the straw debris on the soil

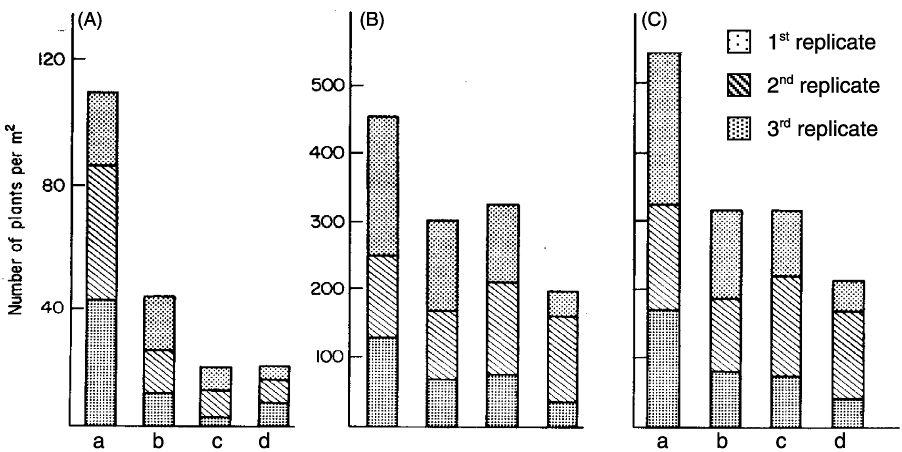

Figure 9.1 Plant Populations on May 19, 1978. (A) First sowing, (B) second sowing, (c) all plants. a. Fumigated inoculated with *L. terrestris* and *A. longa* b. Fumigated and inoculated with *A. caliginosa* and *A. chlorotica*. c. Fumigated: no worms added. d. Not fumigated; no worms added. (From Edwards and Lofty, 1980. With permission.)

Table 9.2 Mean Numbers of Plants Per Plot (per m²) from 1st and 2nd Sowings

Sowing	Treatment[a] A	B	C	D	Standard Error of Mean	Degrees Freedom Error Mean Square	F	F Test
1st	99.0	39.06	18.00	18.00	15.48	6	12.33	Sig < 1%
2nd	457.2	302.4	325.8	208.8	94.68	6	24.34	Sig < 0.5%

[a] Treatments: A. Inoculated with *Lumbricus terrestris* and *Allolobophora longa*. B. Inoculated with *A. caliginosa* and *chlorotica.* C. No earthworms (Fumigated). D. Few earthworms.

Source: From Edwards and Lofty, 1980. With permission.

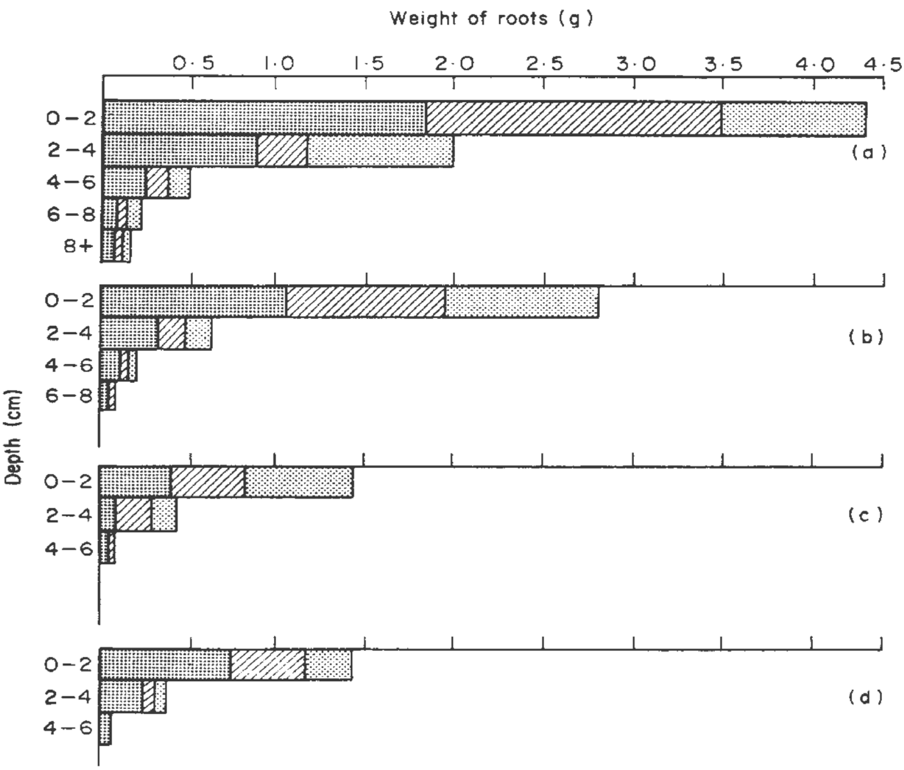

Figure 9.2 Root growth of cereals in soil inoculated with earthworms: (a) *Lumbricus terrestris* and *Allolobophora*, (b) *A. caliginosa* and *A. chlorotica*, (c) fumigated no earthworms, (d) not fumigated few earthworms. Hatching as in Figure 9.1. (From Edwards and Lofty, 1980. With permission.)

surface was incorporated into the soil in the earthworm-inoculated plots, compared with very little incorporation in plots with no earthworms. Cereal yields were also increased significantly by the earthworm inoculations.

In box experiments, a comparison of the influence of natural and simulated earthworm burrows on root growth confirmed that the improved root growth was mainly due to the lining of the burrows. The burrow lining was found to have more

Table 9.3 Mean weight of total root material (g m^{-1} row) of plants relative to earthworm inoculation (1st sowing only) (treatments as for Table 9.1)

Treatment				Standard Error of Mean	Degrees Freedom Error Mean Square	F	F Test
A	B	C	D				
13.3	6.4	3.6	3.4	1.41	6	21.53	Sig < 0.5%

Source: From Edwards and Lofty, 1980. With permission.

available nutrients than the surrounding soil. However, the provision of channels for roots to grow was important. These experiments provide some of the few examples that demonstrate clearly how earthworm activity can contribute to plant and root growth.

9.3.1.6 Direct and Indirect Effects of Tillage on Earthworm Populations

Earthworms are associated with the turning over of large amounts of soil and organic matter.[45,77] Although the extent of this turnover varies widely with ambient conditions, it is estimated that earthworms turn over soil at rates of 2 to 268 tons/ha°, which is equivalent to a gross average of 2 to 5 cm soil depth in temperate agroecosystems.[50] The management of the earthworm's habitat, namely the O, A, and oftentimes B soil horizons, is impacted by tillage down to the depth of the plow. Tillage and cultivations mix and turn over the soil, resulting in temporary, although profound, changes in the soil structure. Nearly all agroecosystems are tilled to some extent, although conservation tillage and no-till (direct sow) is common. Cultivations range in extent from the minimal disturbance of the row openers on a no-till planter through shallow cultivation to the total inversion of soil through deep moldboard plowing. Current conservation practices aim to retain a layer of protective surface crop residue and leave soils minimally disturbed. During tillage earthworms are often brought to the soil surface, which increases their exposure to predation by birds, desiccating conditions, and mechanical damage. However, the degree of physical damage (e.g., dismemberment) appears not to be significant for most earthworm species, compared to the effects of tillage on the incorporation of surface crop residues, which might otherwise provide food resources and protective cover for epigeic species.[83,97]

In experiments on continuous cereals at Rothamsted and Boxworth, populations of earthworms were assessed twice annually from the fourth to eighth years of cropping (Figure 9.3).[54] Earthworm populations were shown to differ considerably in response to different amounts of tillage. The cultivations that were compared were deep plowing, chisel plowing, and no-till. Populations of the deep-burrowing species *Lumbricus terrestris* and *Allolobophora longa* increased in the no-till plots, by comparison decreased by 3.5-fold relative to the no-till numbers in the chisel-plowed plots, and were found 37.3 times less frequently in the deep-plowed plots compared to the no-till plots after 8 years of cultivation (Figure 9.3). Over time, the cultivations had much less effect on populations of the shallow-working earthworm species *Allolobophora caliginosa* and *Allolobophora chlorotica* than on the deep-burrowing species.

In another field experiment, populations of earthworms were assessed in plots that had been plowed and were compared with those in plots under no-till for 2 years after the last plowing and others that had been under no-till for 4 years since

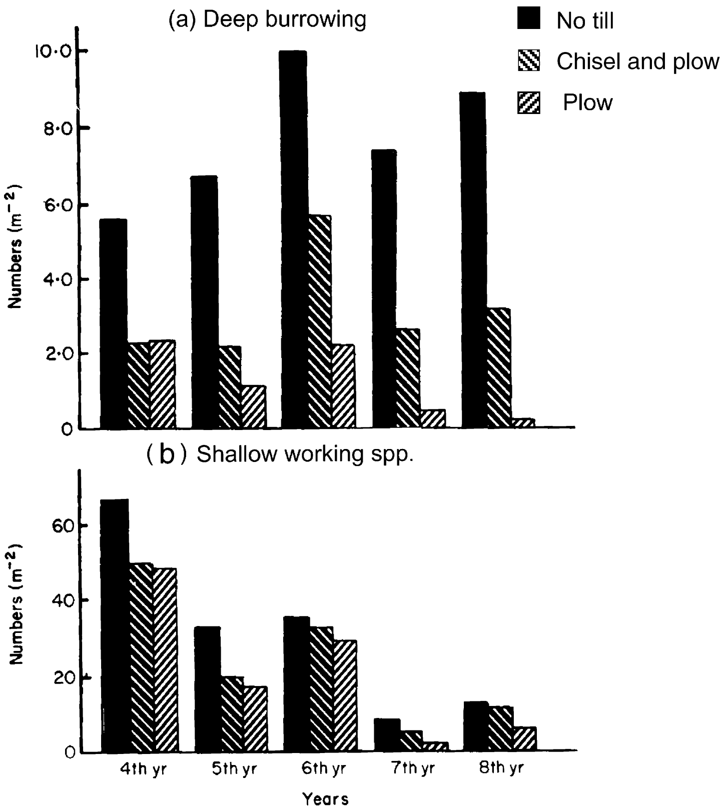

Figure 9.3 Effects of long-term cultivations on earthworm populations—Rothamsted: (a) Deep-burrowing species and (b) shallow working species. (From Edwards and Lofty, 1982. With permission.)

the last plowing. Populations of all species of earthworms were greatest in plots after 4 years of no-till, intermediate (40%) in those under no-till for 2 years, and lowest (20%) in the plowed plots (Figure 9.4).

A survey of earthworm populations in a commercial farm in southeast England compared earthworm populations in seven fields that had been under no-till for several years and seven fields that had been plowed for several years; all fields had been sown with cereals. There were highly significant decreases in populations of *Lumbricus terrestris* and *Aporrectodea longa* in the plowed fields compared with the numbers in the no-till fields (Figure 9.5). Yet there were also smaller decreases in populations of shallow-working species, such as *A. caliginosa* and *A. chlorotica*, due to plowing.

Rotary tillage killed an average of 64% of earthworms in a Swedish ley,[24] with even greater mortality of approximately 10% after subsequent plowing. Interestingly, earthworm populations in the tilled ley recovered to levels in an undisturbed control ley after only 1 year.[24] There was also a change in the earthworm age structure and a decrease in the numbers of species after plowing compared to those in unplowed controls. This agrees with conclusions by Fraser et al.,[60] where only two species,

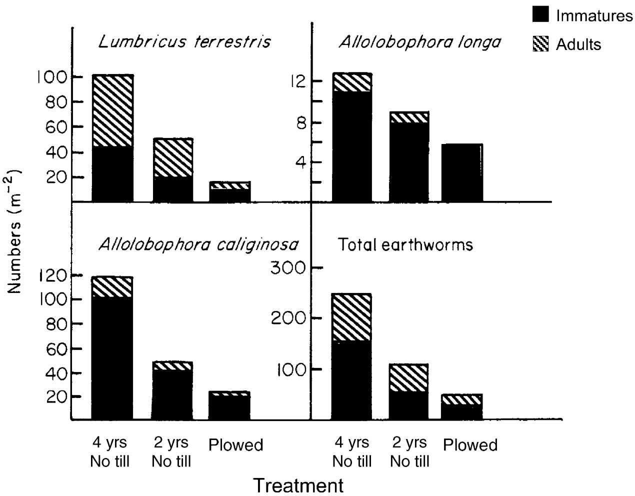

Figure 9.4 Effects of repeated no-till and plowing on earthworm populations. (From Edwards and Lofty, 1982. With permission.)

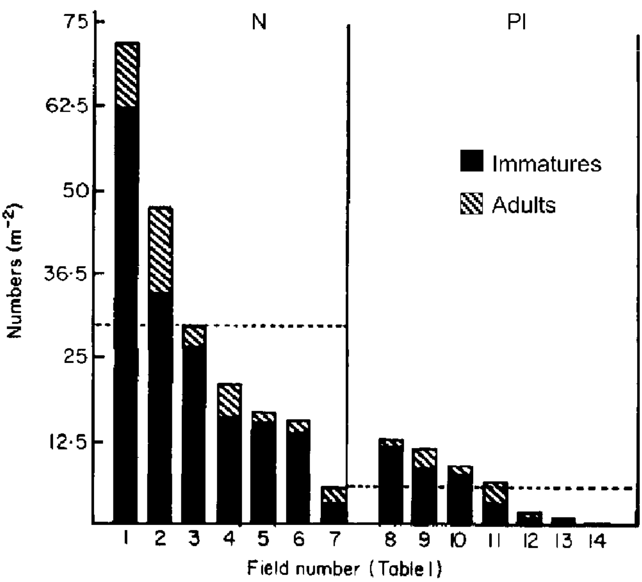

Figure 9.5 Populations of *Lumbricus terrestris* in seven no-till and seven plowed fields on a commercial farm on southeast England. (From Edwards and Lofty, 1982. With permission.)

Aporrectodea caliginosa and *A. trapezoides*, persisted under continuous arable production from an original community composed of five lumbricid species. Fragoso et al.[58] predicted that tillage would promote a decrease in earthworm species richness and of native species in a tropical agroecosystem and increase the abundance of endogeic species compared to an undisturbed soil system. A likely reason for such patterns would be that anecic and epigeic species depend on the maintenance of a surface litter layer, which is not present in all agroecosystems. Although Jimenez et al.[81] reported that endogeic species dominated in undisturbed savannas and anecic species comprised 88% of total earthworm biomass in a man-made pasture, one could argue that the higher levels of organic matter resources in a pasture also stabilizes the habitat for anecic species.

Comparisons of earthworm abundance under no-till and tilled agroecosystems made by Aslam et al.,[3] Carter et al.,[34] Hubbard et al.,[74] Jordan et al.,[83] and Kladivko et al.[88] all confirmed that earthworm populations were generally larger in no-till or conservation-tillage systems under widely differing soil conditions. Additionally, in a survey of earthworm populations under no-till crops in Scandinavian agroecosystems, Rasmussen[121] reported that the majority of species studied increased in abundance with time under no-till. The no-till agroecosystems retained more surface residues over a greater part of the year than those with chisel-till management. Such differences in residue levels can be attributed not only to the type of crops in the rotation but also to decreased frequency and intensity of tillage and the promotion of decomposer food webs. In some ways, the retention of soil invertebrates such as earthworms in a no-till system is sustainable in the long term, since the greater amount of residues, available as food resources, promote earthworm communities that are both rich and diverse. The international trend towards increased adoption of conservation tillage and no-till allows most modern agroecosystems to provide for the foraging requirements of different species of earthworms. Yet this may not always be adequate to also replenish soil organic matter pools in the deeper parts of the soil profile. Therefore, the maintenance of agroecosystem primary productivity through traditional tillage inputs may have to be included in long-term systems with special regard to their interactive effect on organic matter availability, which is key to the retention and maintenance of larger earthworm populations.

9.3.1.7 Interactive Effects of Tillage and Earthworm Activity on Organic Matter Management

Cultivations not only disturb the soil and its inhabitants; they also change the soil organic matter dynamics. The types and amount of plant residues can change from a mixture of higher plants in forests or prairies to residues from a monoculture. Although agroecosystems can integrate a greater number of different crops over several years through rotations, current agricultural management commonly results in a decrease in the type and amounts of plant residues available for consumption by soil organisms. Earthworm communities can influence the spatial distribution of resources by altering their form and availability to mesofauna and microorganisms, thereby regulating nutrient cycling processes.[68,77,95,102] Foraging for litter and burrowing

activities by the anecic species *L. terrestris* to consolidate carbon resources at the surface redistribute these resources through the mineral soil layers.[89]

Many workers have shown that different forms of agricultural management can influence earthworm communities[19,164] by the extent to which surface residues are produced, located, and retained. In terms of organic-matter management, there are two main forces at work in agroecosystems supporting earthworm populations. First are surface-active earthworm species, which comprise the greater proportion of primary decomposer biomass. According to their feeding ecology, earthworms manage residues as a function of, and in response to, the type, amount, and frequency with which biomass is produced in the agroecosystem. Second is the extent to which crop residue biomass is either removed or returned to an agroecosystem. Furthermore, there is a critical balance between the incorporation into soil and retention of surface residues. The amount of raw materials available to support earthworm populations also affects the proportion of residues that are processed to replenish soil organic resources.

Surface residues provide a food source for surface-dwelling earthworms such as *Lumbricus rubellus* (Hoff.) as well as deep-burrowing species like *L. terrestris*, which forages at the surface and pulls organic matter into its burrows. It is well established that most species of earthworms respond positively to additions of organic matter,[50,61,101,117] with an increased activity[38,75] and, in many cases, increased earthworm populations after repeated additions of organic matter to systems. When earthworms encounter organic matter resources, not only do they tend to aggregate in the vicinity of the source,[38] but they may also affect these microsites locally by their specific habits.[75] Earthworm populations also have interactions with the quality of organic-matter inputs. Tian et al.[151] showed that the mean abundance of the tropical species *Hyperiodrilus africanus* and *Eudrilus eugeniae* decreased with mulch quality. However, the issue of food preference is more complex. For example, Tian et al.[151] showed that the activity of *Eudrilus eugeniae* focused on both the best- and poorest-quality organic-matter sources. Doube et al.[49] showed that among *Aporrectodea caliginosa*, *A. longa*, *Lumbricus rubellus*, and *L. terrestris*, all preferred mixtures of organic matter and soil, as opposed to pure sources of either type of food resource.

Over a series of long-term field studies, Mele and Carter[108] observed that agroecosystem management that called for the retention of stubble as a surface mulch promoted the growth and establishment of larger earthworm populations. When crop residues are removed from agroecosystems, earthworm populations tend to decline.[61] Likewise, when organic residues are incorporated into soil, their availability to surface-dwelling earthworm species is decreased.

Although Fraser and Piercy[61] reported that earthworm populations increased with time over the course of 4 years of crop residue incorporation, Mele and Carter[108] reported that the incorporation of stubble decreased earthworm populations by an average of 53%.

The decomposition of crop residues by earthworms[41] is enhanced when they contain lower concentrations of polyphenols, higher proportion of proteins, and a lower C/N ratio compared to those in herbaceous materials in undisturbed ecosystems. A wide range of earthworm consumption rates of organic matter has been reported by various workers. Whalen and Parmelee[160] estimated that earthworms consumed

11.8 to 17.1 Mg ha^{-1} year^{-1} organic matter under similar field conditions. Bohlen et al.[20,21] reported that *L. terrestris* could forage and incorporate 840 Mg ha^{-1} year^{-1}. Raw[122] estimated that *L. terrestris* incorporated orchard leaf litter at a rate of 2 Mg ha^{-1} year^{-1}. In the absence of more extensive data regarding organic matter consumption rates for other earthworm species, perhaps these estimates should be taken as upper limits for turnover.

The mixtures of earthworm species and the placement of organic residues can affect the rates of decomposition and the fate of organic materials. The extent to which tillage promotes organic-matter contact with the soil is a key issue. The microbial decomposition of plant materials is promoted by earthworm activity.[13,50,162] Earthworms are also directly involved with the dispersal of microorganisms through the soil matrix,[49,150,155] expanding the range and types of substrate available to microorganisms and inoculation of macroscopic fractions of organic matter.[150] The decomposition of mechanically soil-incorporated leaf litter in the field was stimulated by inoculation with casts, which are often a primary agent of microbial dispersal in the soil.[39] The interactions among different species of earthworms can lead to uniquely structured earthworm communities. The predominance of species from certain ecological groups thus has an influence on the spatial variability of organic-matter pools. Jegoú et al.[80] reported that the epigeic species *Eisenia andrei* (Levinsen), the anecic *L. terrestris*, the anecic *Aporrectodea giardi*, and the endogeic *A. caliginosa* all redistributed litter carbon such that surface casts, belowground casts, and burrow walls were enriched in carbon more than in bulk soil. Through their habits in foraging and creating middens, epigeic and anecic earthworm species can change the spatial distribution of coarse organic matter at the soil surface and within the soil matrix.[63,80,118,130,131,161] Moreover, in a corn-cropping system, Subler and Kirsch[146] reported that 96% of the total coarse organic matter in the surface soil was concentrated around earthworm middens by early spring, after an autumn corn harvest.

Some earthworm species can influence the spatial variability of soil organic matter near the soil surface through the formation of middens[109] and deposition of raw and processed organic matter in their burrows. Middens are highly localized patches of soil, casts, and coarse organic matter in various stages of decomposition. These structures are hotspots of carbon and nitrogen accumulation, whereas the surrounding (nonmidden) soil is often considerably lower in carbon and nitrogen.[146] Middens are usually approximately 30 to 50 mm in diameter, and it is therefore important to consider small-scale spatial variability associated with earthworm middens.

As foraging activities proceed, earthworms can decrease the area of the soil surface protected by residual coarse organic matter. Without residue cover, the soil surface is vulnerable to degradation by increased exposure to wind or water weathering[62] and may form surface crusts or seals. Another effect of residue consolidation is to increase the spatial heterogeneity of organic carbon resources at the soil surface and within the soil matrix. Earthworm foraging results in a redistribution of the organic resources necessary for the production of carbonaceous transient binding agents.[153] This could limit the availability of these binding agents on small spatial scales and would thereby influence the formation of soil aggregates that are resistant to slaking. The consequences of surface organic-matter foraging by

deep-burrowing species of earthworms could include the exposure of a considerable amount of soil surface area to increased weathering.

9.3.1.8 Earthworm Casts and Their Interactive Effect on Soils and Agroecosystems

Earthworm casts differ sufficiently from the soil from which they are produced to merit a separate discussion. Agroecosystems depend on nutrient recycling to maintain sustainable production and minimize fertilizer inputs. Earthworm casting can contribute significantly to the stabilization of organic matter,[80,103,107] nutrient availability,[69,96,113] and the dispersal of microorganisms.[155] Even with the low levels of earthworm abundance in a nutrient-depleted soil, organic matter and nutrients were brought to the surface in the form of casts by *Pontoscolex corethrurus*.[69] Yet cast composition and stability are dependent on earthworm species composition, populations, depth, agroecosystem inputs, and soil conditions.[29,64] Schrader and Zhang[127] suggested that the more sensitive a soil was to tillage, the more positive the effect that casting would have on formation of water-stable aggregates. However, surface-deposited casts are in their moist state still susceptible to dispersion.[70,96,104,132] Compacted soils tend to promote more casting by earthworms,[11] which may also be concentrated close to the soil surface[12,84,167] and may contribute to further increases in the number of casts dispersed. The dispersal of casts is a form of soil erosion; soil is lost together with nutrients it contains and organic matter. Binet and Le Bayon[11] reported that the spatial distribution of cast material in a row-crop agroecosystem differed in response to compaction. It seems that soil already degraded by compaction may be degraded further, at least at the surface, by dispersed earthworm casts, the constituents of which increase microporosity.

9.3.1.9 Effects of Earthworms on Agroecosystem Nitrogen Cycles

There is a dearth of information on how earthworms affect the cycling of nutrients other than nitrogen and organic-matter pools. However, it has been well established that earthworms are a key regulator in nitrogen cycling and have been found to influence net N mineralization in agroecosystems.[14,40] However, this influence is a function of the timing, direction of transformation, and overall magnitude of N transformations, which are very dependent on N sources.[147] The turnover of dead earthworm biomass can be a major source of mineral N for plants,[160] where plants can take up nearly 70% of N added as earthworm tissue. Agroecosystem nutrient sources and nutrient availability seem to interact strongly with earthworm activity,[15] and this is particularly true for inorganic N sources. Accordingly, the amounts of mineral N available in agroecosystems inoculated with *L. terrestris* were greatest after urea inputs and smallest after calcium nitrate inputs.[67]

Mineral forms of nitrogen in leachates have received much attention due to their widespread detection in groundwater in the Midwest in the U.S. Through their different burrowing habits, earthworms can promote conditions for increased leaching, with a resultant loss of water and dissolved N compounds from an agroecosystem.[15,145] However, the incidence and magnitude of dissolved organic nitrogen (DON)

in leachates has been largely unexplored. Soluble organic substances can enter the soil solution from organic materials that decompose on the surface and within the soil, through leaching of plant root exudates, through the breakdown of organic materials initiated by soil invertebrates, and by the turnover of the soil faunal biomass. Nitrogen can be transformed into DON through the immobilization of fertilizer inorganic N by microorganisms, with subsequent releases of metabolic products and exudates from the microbial biomass. Subler et al.[145] showed that DON was a major component of leachates collected from CSW ridge-till and to a lesser extent in CS chisel-till agroecosystems that had increased activity by deep-burrowing earthworm species such as *L. terrestris*. The production of DON and its pathways through agroecosystems are not well understood. This is particularly true in terms of how deep-burrowing earthworms might affect the production and transport of DON in different agroecosystems.

9.4 CONCLUSIONS

Earthworms are a ubiquitous and important biological component of agroecosystems. Their role in agroecosystems is multifold and similar to that of a biological engineer, since earthworms are integrators of basic soil processes. This integration of soil physical, chemical, and biological features is used by the earthworm to optimize its environment and, incidentially, can serve to improve cropping conditions. The ways in which earthworms can be separated into functional ecological groups require some degree of revision and reinterpretation. The impacts of earthworms on agroecosystems and their reactions to management inputs appear to be less specific than once thought, since earthworm behavior and its overall effects may change with habitat, cropping, and earthworm growth stage. While the roles of earthworms in organism- and community-level processes have been fairly well established, further studies at the agroecosystem level are needed to better elucidate how agricultural management practices might be optimized or take advantage of the activities of earthworms in promoting soil fertility. Although the current literature intimates that particular earthworm species can be pigeonholed into the "box" of a specific process, the complications invited by consideration of interactions among ecosystem-level processes are formidable. Perhaps it is best to consider specifically where and when earthworms cause significant deviations from desired system functions and then to build integrated management recommendations upon observations made from such necessarily long-term studies.

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